Tectonics from fossils? Analysis of reef-coral and sea-urchin distributions from late Cretaceous to Recent, using a new method

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ABSTRACT: Biogeographical distribution is seen as a product of small- and large-scale factors, of which only the latter are important in palaeogeographical reconstruction. We review here previous methods for assessing the historical sequence of major events that have caused biogeographical distributions, and we argue that the most rigorous of these is cladistic biogeography. We also advocate our own new method, which uses parsimony analysis of taxa shared between sample localities. In not being dependent on prior phylogenetic analysis, this method is especially suitable for taxonomic groups which lack an adequate phylogeny.

This new method takes contemporaneous distributional data from one or more narrow stratigraphic time planes (including the present), and generates a cladogram of sample localities for each of them. We interpret these cladograms as hypotheses of historical sequences of divergences between biotas, for which the sample localities provide geographical control. Congruence between cladograms from different organic groups and time planes provides an indication of those events which are most likely to have been the result of major (e.g. tectonic) historical factors. This method avoids prejudgement of areas of endemicity. We also argue that because younger major historical events can destroy the biogeographical patterns produced by older events, we can reach a more complete understanding of historical biogeography by using a combination of Recent and fossil data. The method however requires refinement and we summarize some of its present problems.

We present area cladograms for Recent and Lower Miocene corals and echinoids, and for Eocene and late Cretaceous (Campanian–Maastrichtian) echinoids. Although these should be tested against area cladograms based on other taxa, we conclude, amongst our preliminary results, that: (1) the present Indo-Pacific fauna is a young biogeographical entity, not older than the Lower Miocene; (2) prior to this, Pacific faunas had been isolated since a time older than the Upper Eocene; and (3) the faunas of the Atlantic and western Tethys have been distinct from those of the Indian Ocean and eastern Tethys since a time long before the 'terminal Tethyan event' (Miocene), and since as far back, at least, as the late Mesozoic.

Apart from biostratigraphy, the use of fossils to provide information about geological events has usually been based on direct or indirect assumptions about their autecology. These assumptions and the information derived from them are usually closely worked into interpretations which also use non-organic evidence from facies. In this approach, therefore, fossils are used to reconstruct palaeogeographies as part of facies analysis. Although facies analysis has undoubtedly contributed a great deal to our understanding of Earth history (e.g. by drawing analogies from the present to the past between environments or tectonic settings), the *critical* value of fossil evidence within facies analysis is not always clear. There is a fundamental susceptibility to circularity, because evidence from different sources (such as sedimentology, tectonic information, sea-floor magnetic anomalies, and the fossils themselves) is not always kept independent. How, for example, do we infer, and independently test, whether an extinct organism had a tropical shallow-water distribution?

By contrast, most biogeographers working on Recent biotas use presence/absence distributional data in order to discover regional patterns. Although palaeontologists have also used such methods, they have done so relatively infrequently (e.g. Whittington and Hughes 1972). Methods which use only presence/absence data are best, however, because such data lend themselves readily to rigorous methods of analysis, independently of any other evidence.

In presenting this paper, we have borne in mind the context of the original Symposium and the disciplinary range of its likely readership, and have tried to explain our own and other methods so that they might also be of interest to non-biogeographers.

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4. We have assumed that each area supports similar-sized biotas.

5. We have assumed that our areas are adequately sampled.

For simplicity, the symbols representing biotas also correspond with areas, which implies that our sample localities are always of the same geographical extent as the biotas. (Such sampling would not be possible in practice.) These 'areas' are therefore not necessarily geographically constant entities between time horizons.

In our model (Fig. 2), each divergence event results in two daughter biotas that have a proportion of taxa in common, inherited from their

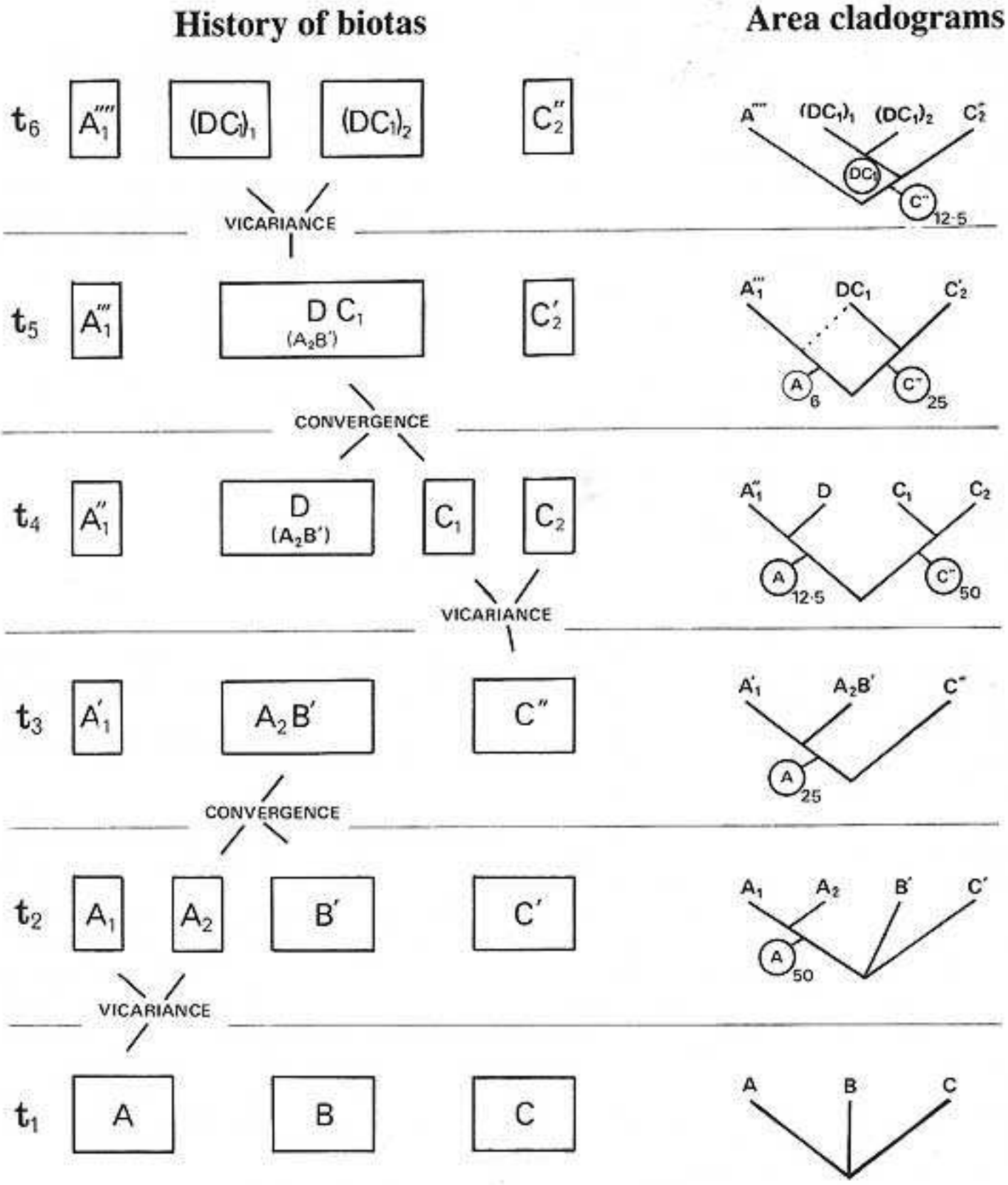

FIG. 2. A hypothetical history of biotas and the corresponding sample locality cladograms, constructed using the rate of biotic turnover shown in Fig. 1. t_1–t_6 = successive time planes. Geographical sample localities are depicted as rectangles, biotas as letters (biotas are assumed to be fully sampled). The initial faunas A,B,C have no taxa in common. Other symbols: C, C′, C″, etc. = turnover of biota C through time; D = endemic element of biota developing after convergence event producing A_2 and B′ faunal mixing. In the area cladograms the common elements of biota shared between sister localities are circled, and the percentage of the total biota shared at the vicariance event that has survived to this time, is also given.

ancestral biota before it became divided. This shared biota acts as a biotic fingerprint to historical kinship of biotas. Through time, however, this fingerprint becomes weaker and weaker, as old taxa become extinct and new ones arise. So for example, the biota common to A_1 and A_2 (i.e. biota A, just prior to divergence t_1/t_2) diminishes through biotic turnover until a later major event (in this case the convergence at t_4/t_5) completely masks the A-fingerprint on the biota DC_1.

Convergence events bring about biotic intermixing, which in geological terms is relatively rapid. Evolution continues within this mixed biota, resulting in the appearance of new taxa within the area which contains this composite biota. New taxa are confined to this area by these most recent biogeographical barriers. Some or all of these taxa may even have originated vicariously in direct response to these barriers. This development of endemicity probably takes place over a longer time span than intermixing, but it remains until disrupted by further events.

Reference to Fig. 2 shows how this process would be seen by PAE cladograms. A newly intermixed biota is linked as a sister-biota to the descendant of whichever pre-convergence biota underwent *divergence* more recently, because this biota bears the stronger fingerprint (i.e. shares more taxa with the newly intermixed biota). For example, in the t_4/t_5 convergence, biota DC_1 shares 25 per cent of its taxa with C″ but only 6 per cent with A, divergence of which (at t_1/t_2) was geologically older than divergence of C″ (at t_3/t_4). Convergences themselves are not shown graphically by the cladograms, but in practice, they can be inferred by comparing cladograms over a time sequence, if between any pair of successive time intervals there is a transposition of sister relationships between three biotas. In Fig. 2, the biota D is sister to biota A_1″ at time t_4, but has switched to being sister of the C-lineage biotas at time t_5, following the convergence at t_4/t_5. The two biotas which have intermixed can be identified as: (1) the transposed biota, e.g. D (in DC_1); and (2) its sister biota, e.g. C (in C_2'), though the cladogram only shows a divergence between them.

It is also possible to relate information derived from data on one stratigraphic time plane, to information from a slightly lower one. This makes it possible for histories inferred for different time planes to be used to corroborate each other, and also recovers information 'lost' through geological time (see p. 277; also Grande (1985) for a cladistic biogeographical equivalent; but for a rejection of Grande's unpublished earlier version of this, see Humphries and Parenti, 1986, pp. 60–4). The minimum time interval between time planes used in this way should be appropriate to the taxonomic level of the data being analysed. Stratigraphic subzones, for instance, would probably be inappropriate for generic data. There will also be a maximum time interval. The main consideration in choice of interval is that of the evolutionary turnover rates for the taxa concerned. This multiple time-plane approach introduces a synoptic approach, in conjunction with the outright historical interpretation of biotas of a single horizon already outlined.

Fig. 2 illustrates how this works. The record of the divergent event which affected biota C″ at time t_3/t_4 is retained through t_5 to time t_5/t_6, where one of its daughter biotas, C_1 (in DC_1) becomes divided again. (Note that in the more recent cladogram (t_6), the older event is to be found nearer the origin of the cladogram than the more recent event.) Thus, the same divergence may appear in cladograms from more than one time plane, with successive divergences displacing each other further down the cladograms through geological time. The same is true for the indirect record of convergences.

Thus, PAE cladograms at all times produce a nested series of biotas, as sampled at particular localities, based only on how recently they have had taxa in common, irrespective of the nature of the historical events. Indeed, it is quite fallacious to use the cladograms as a direct record of vicariance events. A direct reading of the cladogram at time t_6 in Fig. 2, for example, would suggest that all four biotas were united at some time in the past, whereas this is obviously not the case. PAE cladograms only give a graphically direct representation of historical events if there have been no convergences. Nonetheless, each cladogram, interpreted only as a representation of the history (i.e. relative recency of biotic intermixing) of *biotas*, as represented at sample localities, is accurate. It can also be read as an *area* history, by reference to the localities at which the biotas have been sampled, and the pattern in which they are grouped, as discussed in the next section.

Interpretation: (2) areas, time planes, and Earth history

The final step, having inferred a history of biotas as soundly as the data permit, is to translate it into implications for Earth history and palaeogeographical reconstructions. Taken on their

own, the cladograms only provide historical hypotheses about biotas—as represented at particular sample localities—in terms of recency of intermixing between these localities. Nevertheless, divergences in cladograms can be read as hypothetical vicariance events, and these imply that barriers to biotic exchange might have appeared somewhere in regions which lie between pairs of sister-sample localities on each side of a divergence.

It is not possible, however, to go further and hypothesize the nature of these barriers or the nature of the events concerned, without introducing major assumptions. Neither can the closeness of relationship between sample localities be used to infer either the 'effectiveness' of the barriers (cf. 'filter barriers') between them, or the palaeogeographical proximity of sample localities. There is, for example, no way of knowing whether a divergence event, affecting shallow-marine groups of organisms, was due to the appearance of a land barrier, to some kind of oceanographic event such as a change in cur rent configurations, or a general widening of oceanic separation between the localities concerned. There is obviously a whole range of possible Earth history events that could account for vicariance and intermixing, these being essentially tectonic, eustatic, climatic, or oceanographic ('TECO' events of B. R. Rosen 1984), singly or in combination (e.g. tectonoeustasy).

Since the nature of barriers and events cannot be specified from parsimony analysis of distributions alone, or in fact from any other analysis of presence/absence distributional data (such as cladistic biogeography or cluster analysis), and since histories inferred from these methods cannot be used as rigorous tests of geological events, or vice versa (Patterson 1983), the main role of biogeographical analysis lies in making test-like comparisons with independently derived histories. This limitation of biogeographical analysis is illustrated by Williams' work (1969, 1973) on the distribution of Lower Palaeozoic brachiopods, in which he was able to fit the same set of cluster analyses into two totally different, independently derived palaeogeographical reconstructions (though part of the problem is attributable to the nature of phenetics; p. 279)). Of course, if no independently derived model of geological events or palaeogeography is available, a biotic event inferred from biogeographical analyses can be used as a palaeogeographical pointer to further research. Well-corroborated biotic distribution histories have stimulus value for those working in other related subjects, and invite explanations (e.g. Humphries and Parenti (1986) on Pacific history and bipolar distributions).

If it seems somewhat discouraging that analytical historical biogeography cannot be used to test geological models, a saving consideration may lie in introducing some basic ecological considerations. For instance, if—as here—we know that we are dealing only with shallow-water marine organisms, then this slightly constrains the range of possible barriers and 'TECO events' implied by the locality cladograms. A different range of possibilities would be implied by results based on terrestrial organisms, though we should expect patterns derived from marine and terrestrial organisms to be complementary (Hallam 1983). Set against this, is that the ecology (especially the habitat and dispersion ecology) of the groups concerned has to be assumed for fossil organisms, although some ecological assumptions will obviously be safer than others.

An important part of interpreting biotic histories is the handling of areas and sample localities, and it can also introduce a subjective element. Although sample localities can be as geographically confined or broad as we wish, each one should be large enough, ideally, to encompass the complete range of local habitats. This would minimize parsimony differentiation between sample localities, which arises from local habitat preferences of organisms rather than historical events. Lambshead and Paterson (1986) have used a method similar to our own for ecological analysis. In practice, complete elimination of habitat factors is probably impossible at the sampling stage, and is best achieved by relying on the congruence approach, in comparing as many different cladograms as possible. Even this may not eliminate regional ecological factors (see p. 288).

Sample localities can therefore be arbitrary in size, and it may be most convenient to use a grid or, as here, outcrop areas for fossil biotas, and island groups for living biotas. Alternatively, a locality set could be devised with a particular geological history in mind, in order to provide a direct, independent test-like comparison with the hypotheses derived from biotas. Tectonic features, like plate boundaries, crustal sutures, suspect terranes, and ocean/continent boundaries (at the present day or conjectural in the past) can be used to define a sample locality set for investigating a tectonic history, and similar schemes could be devised for other TECO events.

If localities have not been grouped beforehand against the background of a particular

independently derived history, the problem of grouping localities can arise again after initial analysis, since the resulting sample locality cladograms may be too locality-specific to be useful or comprehensible. Grouping may also be helpful, at the risk of loss of real differences of history—if distributional information from different organisms is based on similar but not identical localities—by designating areas which accommodate differences in the locality sets. The task of grouping may be made easier at this stage by considerations of congruence between the distributional analyses of different organisms, since there will probably only be congruence for parts of the locality sets.

Thus, although choice and grouping of areas and localities introduces an arbitrary and subjective element into PAE, it is offset by the fact that it can be made explicit, and that it should be acceptable so long as it is used experimentally for test-like comparisons with independently derived models.

A similar problem arises with choice of stratigraphic horizons. As with localities, there are arbitrary factors in the choice. The *interval* between horizons is discussed on p. 285. There is also *time span* of the sample horizon to consider (subzone, zone, stage, etc., or an absolute time span), because it is not possible to take a true instant of time as a sample base in geology, other than the present. As with time intervals, choice of span will be affected by available stratigraphic resolution, and the evolutionary rates in the organisms concerned. Note that each cladogram carries historical information, which in theory should cover a span of time as far back as the stratigraphically oldest taxon in the data set (Figs 1 and 2), though in practice probably only as far back as the average survivorship duration within the taxonomic group concerned. On the other hand, of course, inferred events cannot be younger than the uppermost level of the most recent stratigraphic horizon used in an analysis.

Use of time spans implies that the distributional records which make up a particular data set must be an integration of occurrences which are scattered throughout the time span, and this may be as long as several million years, depending on choice of horizon. Use of congruence should help to eliminate some of the effects of stratigraphic scatter on individual cladograms. As with areas, choice of actual horizon, and of time span, can be made for comparison with an independently derived history, or be neutral and heuristic. There is scope for establishing stratigraphic constraints by analysing the ages of individual taxa on which a particular grouping of two or more localities is based, but we have not explored this here.

We have assumed here that all biotic divergences identified in a cladogram followed geologically soon after the major events that caused them, but this may not always have been true. Moreover, vicariant differentiation of taxa acts at the species level and presumably has a progressively longer time-lag in its effect at successively higher taxonomic levels. If, for example, genera are analysed (as here) we may have to bear in mind the possibility of a significant time-lag between a geological event and its resulting biotic event. Indeed, we have no data even for the species-level time-lag, though it is probably related to evolutionary rates—but varies with the actual taxa and events concerned. In other words, although PAE produces a history of possible events, we cannot judge what their actual date and their time resolution are. This needs to be borne in mind when making comparisons with geologically derived histories whose stratigraphic control is often better known and more precise. For convenience we have summarized our assumptions in using PAE in Table 2.

Some currently unresolved problems of PAE

Although PAE has parallels with cladistic analysis in phylogenetic reconstruction, there are a number of significant differences which create problems for interpreting sample locality cladograms in biogeographical terms.

1. by direct analogy with cladistic phylogenetic reconstruction, all absences of taxa from a biogeographical data set should be treated as unknown character states (i.e. the taxon may genuinely be absent or may be present but as yet undiscovered). We have had to assume, however, that all absences of taxa from faunal lists are genuine, and thus our method suffers from the same problems of sampling bias and ambiguity in its data set, as in all methods other than cladistic biogeography. Although it seems to us that our assumption will provide a reasonable approximation to the true state of distributions, when dealing with well-studied groups with a good fossil record, certainly, this cannot always be the case.

2. whereas non-congruence in a phylogenetic cladogram is explained by postulating convergence, parallelism and non-homology in some characters, non-congruence in our biogeographical analyses implies that one or more

TABLE 2. *Summary of parsimony analysis of shared presences method and the assumptions involved*

A. Data

1. Taxon distributions form an overlapping mosaic which changes through geological time due to historical factors.
2. Fossil record, though incomplete, is a biogeographical sample which carries vestigial biogeographical 'signals' and which can be analysed by rational methods to produce testable historical hypotheses.
3. Biogeographical mosaics (present or past) can be analysed by sampling them at particular points (sample localities) within a particular stratigraphic horizon, using taxonomic lists of 'presences' (i.e. without prior need to identify ranges or areas of endemicity).
4. Choice of sample localities can be arbitrary or made for direct comparison with an existing independent biogeographical hypothesis.
5. Taxa used for analysis are non-polyphyletic.
6. Time factors mask older events, making it necessary to use sequences of data based on different stratigraphic horizons (synoptic approach) to maximize use of information in fossil record.
7. Stratigraphic control is adequate.

B. Method

1. Shared presences of taxa between sample localities can be analysed like homologies (synapomorphies) in phylogenetics, and sample localities can be treated like taxa in phylogenetics, to give sample locality cladograms.
2. Lundberg rooting (hypothetical sample locality with no taxa present) gives historical basis for interpreting sample locality cladograms, i.e. presence of a taxon is more biogeographically 'advanced' than absence.
3. Parsimony is the only criterion for choosing between competing biotic histories.

C. Results

1. Sample locality cladograms represent historical hypotheses about relative recency of biotic exchange between sample localities.
2. Suites of shared presences between sample localities represent biogeographical assemblages (or biotas).
3. Dichotomies (nodes) in sample locality cladograms represent divergence events between biotas. (Convergences are not shown but are not precluded.)
4. Age of all events, within a particular cladogram for a particular horizon, must lie within the age of the oldest taxon used in the analysis and the youngest horizon from which data were taken.

D. Interpretation

1. There are two biogeographical models for interpreting divergences: random events and major events disrupting whole biotas, e.g. due to appearance of a new barrier (vicariance).
2. Non-congruence within a single data set is produced either by convergence of biotas, or by localized extinctions and clade-specific dispersal, both of which act to mask or destroy any pre-existing divergence pattern.
3. Congruence of sample locality cladograms between different groups of organisms at the same geological horizon suggests that extrinsic events have affected the biota. Lack of congruence points to other kinds of events (e.g. dispersal) or other factors (e.g. poor stratigraphic control).
4. Probability of congruence is maximized by choosing groups which share similar broad ecological characteristics, though this introduces extra (ecological) assumptions into the analysis of fossil distributions.
5. Hypothesized vicariance events represent the appearance of biogeographical barriers which lie (or lay) in areas between the sample localities concerned.
6. The nature of biogeographical barriers is not deducible from sample locality cladograms, without also using ecological features of the group concerned (which introduces extra assumptions into the analysis).
7. Palaeogeographical distances (e.g. between biotas, or barriers, or areas), whether relative or absolute, cannot be deduced from sample locality cladograms alone.

of our taxa (cf. characters in phylogenetics) may have originated independently at several times or places. Although a few taxa may genuinely be polyphyletic, we doubt if this would be a significant feature of the data base, and have assumed that our taxa are largely non-polyphyletic. We believe that the best solution to this problem in future work is to calculate the most parsimonious cladogram, using Dollo's Law (Farris 1977), an option that is available in some numerical cladistic programs, but one which we have not yet tried. According to this rule, taxonomic characters are transformed from 0 to 1 only once (i.e. in PAE, taxa evolve only once), but may be transformed from 1 to 0, as often as is required (i.e. a taxon can be lost from as many sample localities as necessary).

3. as already discussed, there is the problem of rooting and the interpretation of the sample locality pattern. By using Lundberg rooting, which we feel is the current best option, we cannot eliminate the possibility that PAE cladograms may reflect, either wholly or in part, latitudinal or other major ecological gradients. A nested hierarchy of sample localities showing a pectinated arrangement (e.g. Fig. 3: Indo-West Pacific to New Zealand in the echinoid cladogram) can be produced by an ecological diversity gradient on a large or global scale, such as latitude, to the same degree as by a historical sequence of vicariance events. Thus, these kinds of ecological effects and historical factors are impossible to separate when PAE produces pectinated patterns, without recourse to additional assumptions or reasoning. Furthermore, areas with small biotas, whether due to ecological gradients or collection failure, will inevitably appear as primitive in the sample locality cladograms. A successively dichotomous arrangement of localities, however, indicates that pairs of sister-areas do have their own unique endemicity, which cannot easily be explained in terms of diversity gradients. An interim solution is to group all localities that occur within a pectinated set together—into a larger area which embraces them, or otherwise discount, provisionally, all events suggested by divergences within the set.

4. although PAE seems, in the end, to settle for quantity rather than quality of data, the resultant cladograms do provide the best-corroborated hierarchy of sample localities using available data on shared endemic taxa, and they therefore provide working hypotheses to be tested further.

Data for the present study

In our study, we have chosen to work at the level of genus, as this is the lowest feasible taxon to use on the global scale we are interested in, and higher taxonomic levels are even less reliably monophyletic. Data on echinoid distributions were assembled for the present day, early Miocene, mid- to late Eocene and late Cretaceous (Campanian/Maastrichtian) times. The data on Recent distribution pertain only to Clypeasteroida and are taken from Ghiold and Hoffman (1986). Other data sets are for total echinoid faunas and were compiled from published monographs, supplemented by data from the collections of the British Museum (Natural History) (see Appendix). Where monographs predate the *Treatise on Invertebrate Palaeontology*, generic determinations were amended where necessary.

Reef-coral data were assembled for the Recent, Lower Miocene, and Upper Jurassic. For the Recent analysis, these were almost entirely from an unpublished table kindly made available by Professor John Wells (Cornell University), compiled and continually updated by him from publications and from unpublished lists sent to him by numerous coral workers. The Recent localities used here include the same lists for the eighteen circum-tropical localities that B. R. Rosen (1984, 1985) used in previous papers. For the Lower Miocene, the coral data used here were originally assembled in order to examine the biotic affinities of an important new Iranian collection (B. R. Rosen and Darrell, in press) with respect to Miocene closure of Tethys in the Middle East. It is for this reason that the localities are relatively close together in the south-west Asia area. For other Miocene areas, see Appendix. Upper Jurassic data were taken directly from Beauvais (1973).

Results

Presentation

The results are presented in two forms, firstly as cladograms of the actual sample areas, and secondly as simplified cladograms based on the shared congruent elements of all the cladograms for a particular horizon (Figs 3–6). These congruent cladograms are labelled with broad regional names, representing groupings of the original sample areas, our exact choice of naming being essentially arbitrary (with some awareness of current palaeogeographical hypotheses).

We will also use these names throughout the following sections. It is, however, important to realize that they imply extrapolation from our sample points to broader areas which include them, and this by itself may tend to blur the very relationships that we are trying to establish rigorously. Our use of 'Pacific' and related geographical terms, for instance, are generalizations based on relatively few sample localities, and we hope that these can be made more precise in future work.

The results are no more than a preliminary attempt to use generic distribution data to identify possible palaeogeographical events from mid-Cretaceous onwards, in a rigorous way that can be tested by further work. All results must be treated as provisional. For the Recent and Lower Miocene sediments the two data sets, one for echinoids and the other for corals, together provide a certain amount of congruence. Similarly, there is some corroboration between cladograms from successive time planes. Although in the following section we emphasize only those events for which we have a limited amount of corroboration, we also mention other possible events and show how this kind of area cladogram can be interpreted.

These results can be regarded in two ways. Firstly, statically, as indicators of endemic patterns at each time plane, and secondly, dynamically, as historical hypotheses. The endemic patterns that are revealed by this method are hierarchical and use all of the available data, in marked contrast to many palaeontological faunal and floral provinces (see p. 278).

Recent data (Fig. 3)

Both analyses of echinoids and reef corals gave reasonably high consistency indices (0.61 and 0.65). Comparison of coral and echinoid data gives a high degree of congruence, with the Indo-West Pacific, West Indian Ocean, and Mid-Pacific grouped together and unresolvable on current evidence. An interesting exception, however, is that the affinities of East Pacific echinoids lie with the Caribbean (a pattern that is well established for numerous other organisms; see examples in Humphries and Parenti 1986), whereas the East Pacific corals are apparently more closely allied to the rest of the Indo-Pacific. This may be an example of one group (reef corals) which has had a distinctive history for ecological reasons.

These analyses of the Recent faunas are especially important, because they can be compared with the observable geography of today to give a qualitative notion of how accurately our results reflect modern geography. It is reassuring, for example, that they clearly reveal the importance of the two main land barriers that lie across low latitudes: the Americas and Eurasia–Africa. But, notably, they also show that in each of the two respective major oceanic regions separated by those barriers (the Atlantic and Indo-Pacific) there are also subsidiary endemic areas. These areas presumably reflect biogeographical barriers, but it is important to note that the barriers do not correspond with any likely landmasses, either now or in the recent past, except possibly along the line defined by south-east Asia–Indonesia–Australia (B. R. Rosen 1984). For interpreting past events from fossil distributions, these intra-oceanic barriers suggest that it is possible to have a complex system of partial ('filter'?) barriers, which is not readily specifiable in tangible geographical terms, within a single (albeit large) marine basin. They also demonstrate the possibility of mid-oceanic vicariance, which is of interest with respect to Hallam's (1978) question: 'How is speciation promoted in an equable shallow marine environment?'

Historical interpretation of these Recent area cladograms suggests a sequence in which the Atlantic and Indo-Pacific first became separated from each other. For the echinoids at least, the faunas of the East Pacific and north-eastern Pacific were at this stage still part of the Atlantic group. Following this major divergence there was, within each main oceanic region, a series of as yet uncorroborated vicariance events, in which the Eastern Pacific and north-eastern Pacific also became separated from the Atlantic. For the reef corals and for Indo-Pacific echinoids, these later divergent events were like the splitting away of successively less remote areas, similar to onion layers, from the 'core' regions of the Caribbean and Indo-West Pacific. Some of this pattern, however, may reflect the small sample sizes in the more outlying areas (e.g. for corals, Cocos-Keeling, East Pacific, Bermuda, Brazil, East Atlantic, and Persian Gulf), since PAE interprets small biotas as 'primitive'. The pattern may, therefore, represent instead the effect of ecological gradients (p. 282).

Lower Miocene data (Fig. 4)

The consistency indices are somewhat lower than for Recent data (0.43 and 0.51), but the two area cladograms are largely congruent. Allowing for the smaller number of sample areas, the

provincial patterns of the Lower Miocene correspond with the present-day analyses in showing an important break in the Eurasia–Africa region. This separates an Indian Ocean and eastern Tethys fauna (Indonesia, Iran, East Africa, Madagascar, and West Pakistan) from an Atlantic and western Tethys fauna (Mediterranean and Caribbean). However, compared with the present day, the Pacific appears as a very distinct fauna, rather than as part of an Indo-Pacific whole. The eastern Tethys and Indian Ocean, when together, have shared a common fauna at more recent times, than either area has with the Pacific.

Historical interpretation of this pattern suggests that the oldest detectable vicariance event separated the Pacific fauna from a Tethyan fauna (Atlantic, Mediterranean and Indian Ocean). The eastern Tethys plus the Indian Ocean then separated from the western Tethys along a line that apparently lay between present-day Saudi Arabia (with its Mediterranean

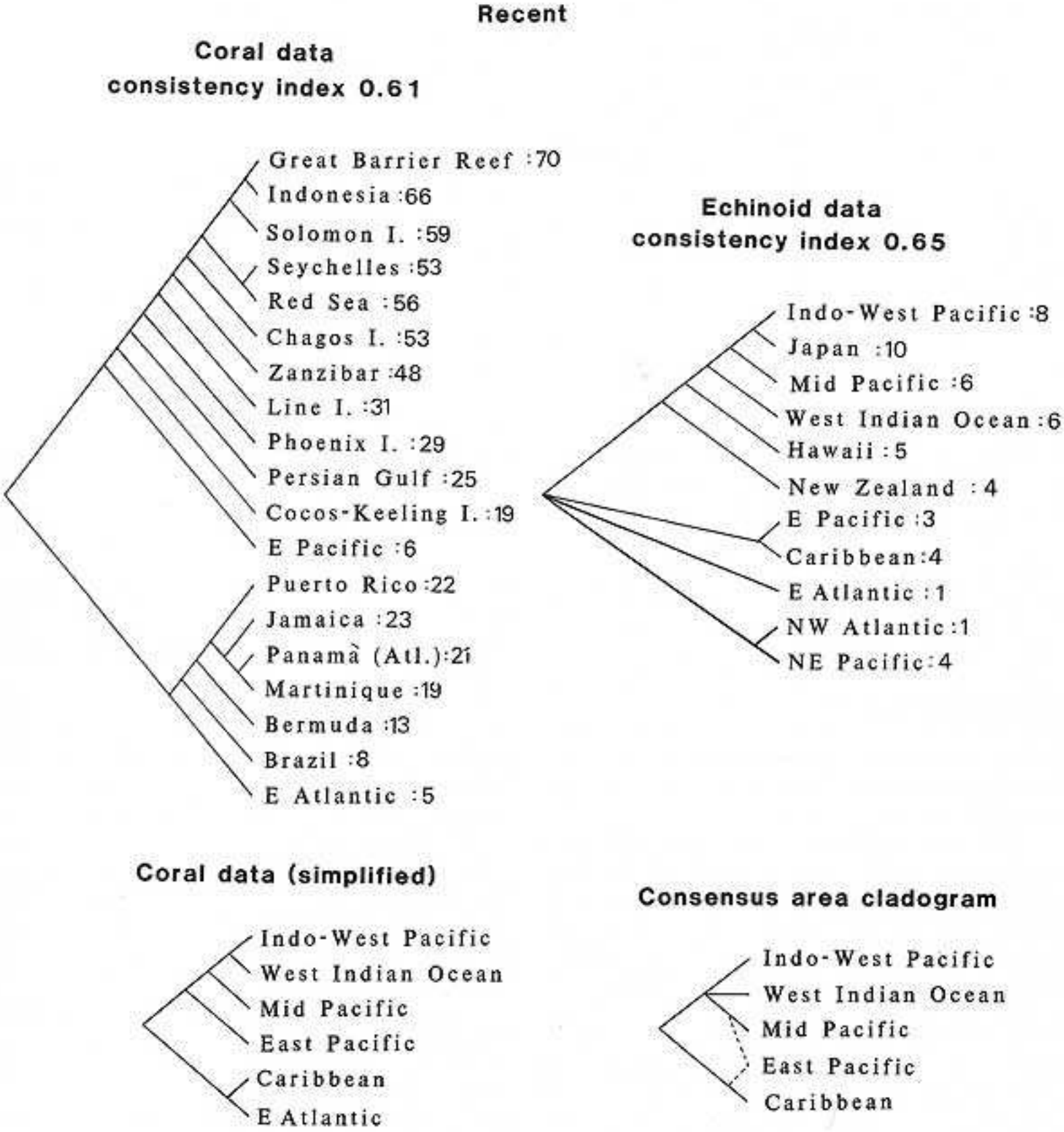

FIG. 3. Sample locality cladograms for Recent distributions of reef corals and clypeasteroid echinoids, and a consensus area cladogram showing only those elements that are common to both cladograms. More than fifty equally parsimonious trees were found for the echinoid data, hence the basal polychotomy in the cladogram. Numbers after sample localities refer to the number of taxa present that are also found in at least one other sample area.

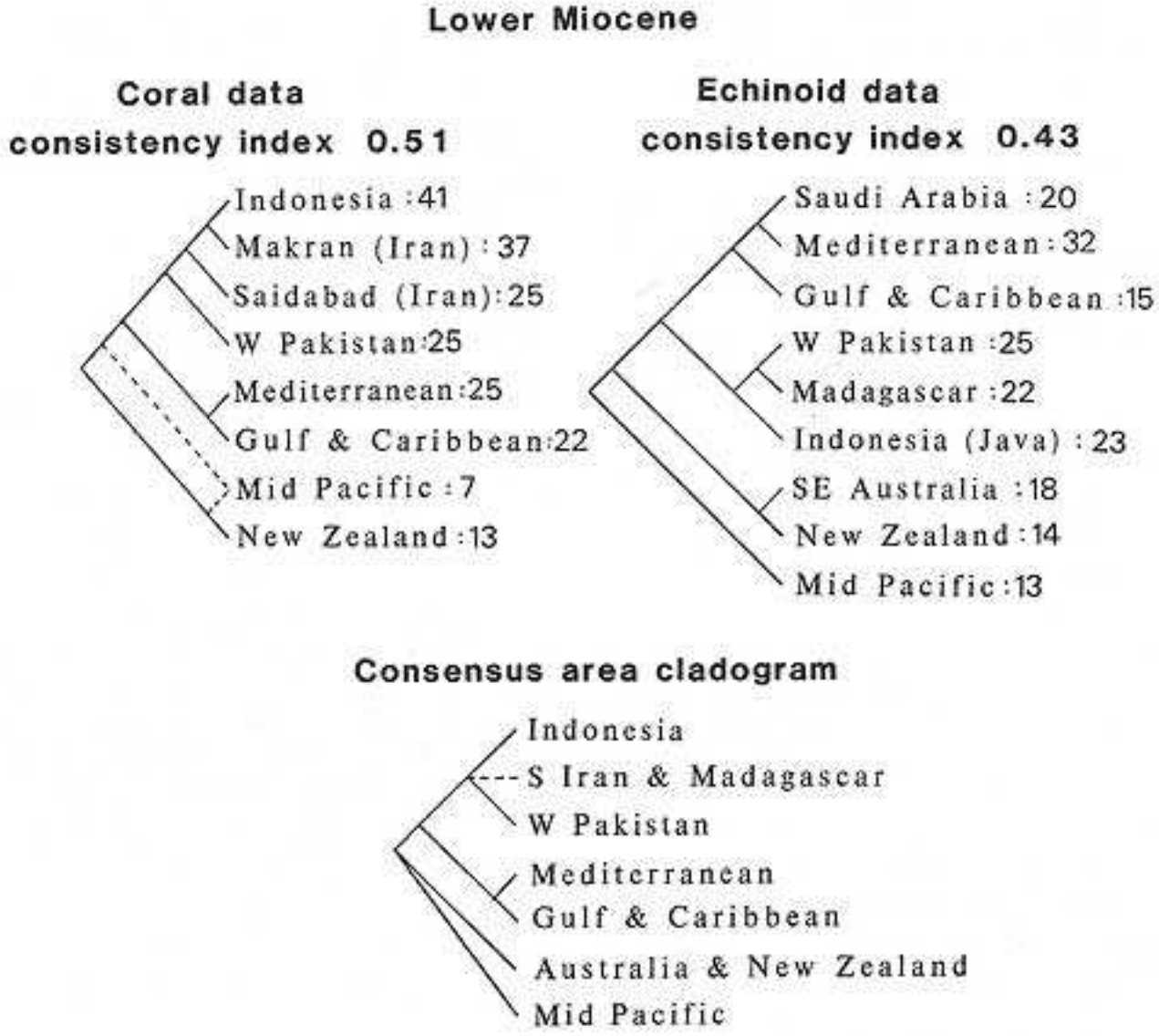

FIG. 4. The most parsimonious sample locality cladograms for Lower Miocene distributions of reef corals and shallow-water echinoids, and a consensus area cladogram showing only those elements that are common to both. Significance of numbers after localities is as for Fig. 3.

echinoid affinities) and Central Iran (with its West Pakistan–Indonesian coral affinities), although this needs further corroboration. The most recent events, with respect to the Lower Miocene, are the divergences within eastern and western Tethys respectively. The most notable of these is between the Caribbean and Mediterranean, a vicariance event that is also seen in the Recent area cladograms.

Although the coral and echinoid data give support to each other through partial congruence, further independent corroboration comes through comparison with the Recent results, since the essentially Atlantic–Indian Ocean, or eastern–western Tethys divergence is common to both sets of results. From the ages of the faunas used, this vicariance event must be older than the end of the Lower Miocene, and probably older than Burdigalian. (Evidence presented later suggests that the history of this divergence may be considerably older.) This in turn implies that, at this taxonomic level, the Recent cladograms have a historical 'depth' of over 20 million years, supporting our earlier surmises based on taxonomic longevity. (Our two geologically older cladograms, however, are for echinoids only, which, on survivorship grounds (p. 277), should have less 'depth' than the coral ones.)

For the Tethys–Pacific vicariance event, there is no congruence support from the Recent analysis. We might have expected to see this below the oldest divergence of the Recent analysis, so it may simply be too old an event to have left its trace on Recent distributions. Indeed, the same divergence does appear as the youngest vicariance event in the Eocene analysis (below), suggesting that it is of late Cretaceous to Palaeocene age. Hence, its absence from the Recent analyses is much more likely to be due to overprinting by later convergence events, which brought the Indian and Pacific Ocean faunas together to make the modern Indo-Pacific grouping. This is supported by the apparent switch in sister-area relationships of the Pacific fauna on the area cladograms between the two time periods. We conclude that the Indo-Pacific fauna (as an assemblage) is itself relatively young, and resulted from a post-Lower Miocene convergence event or events, though of course

this does not imply that all the taxa within that region are as young.

Middle to Upper Eocene data (Fig. 5)

Only one data set is available, producing two trees with a consistency index of 0.5. This is the first analysis in our order of treatment to show a vicariance pattern which is not directly recognizable with respect to the modern Earth. It poses a particular problem, in that the Indian Ocean localities are divided into two pairs, one of which (West Pakistan and Madagascar) has had faunal exchange with the Mediterranean region of Europe in the more recent past than it has had with its closer (modern) neighbour pair in the Indian Ocean (Somalia and eastern Arabia). Yet this second pair today lies between Europe and the first pair, thus appearing like some kind of biogeographical 'island'. Madagascar, moreover, is grouped with West Pakistan, whereas today it lies closer to Somalia. These apparent problems, and any relationships which they might reflect concerning plate movements, can only be resolved with further analyses. They may reflect the inadequacy of data taken from older systematic works, or could be an artefact produced by stratigraphic differences between the faunas being compared.

The Indian Ocean and Mediterranean group is separated as a unit from a transatlantic pair (southern USA with the Caribbean, and Senegal), suggesting a latitudinal difference within the Atlantic and its adjacent seas. The two Pacific localities (south-east Australia and Mid-Pacific) are separated from all other regions—as in the Lower Miocene area cladograms—but possibly because they contain only a few taxa. Similarly, a separation of Tethyan localities on either side of the present Middle East, as for the Lower Miocene data, is also apparent.

From a historical point of view, therefore, this Pacific distinctiveness implies an event which we can be slightly more confident about. It represents a divergence, probably pre-Eocene (see above), between the combined eastern Tethys/Indian Ocean and part of the Pacific. Two other divergences correspond less precisely with cladograms of other ages. The intra-Atlantic latitudinal divergence also appears in the late Cretaceous results, and the broadly Middle East, intra-Tethyan divergence occurs in both the late Cretaceous and early Miocene data. The relative timing of these events (if, that is, they are not simply latitudinal gradients) in each area cladogram is, however, not the same, so one of them (the intra-Tethyan event) may have occurred twice, once in the late Cretaceous or before and once between the latest Cretaceous and earliest middle Eocene.

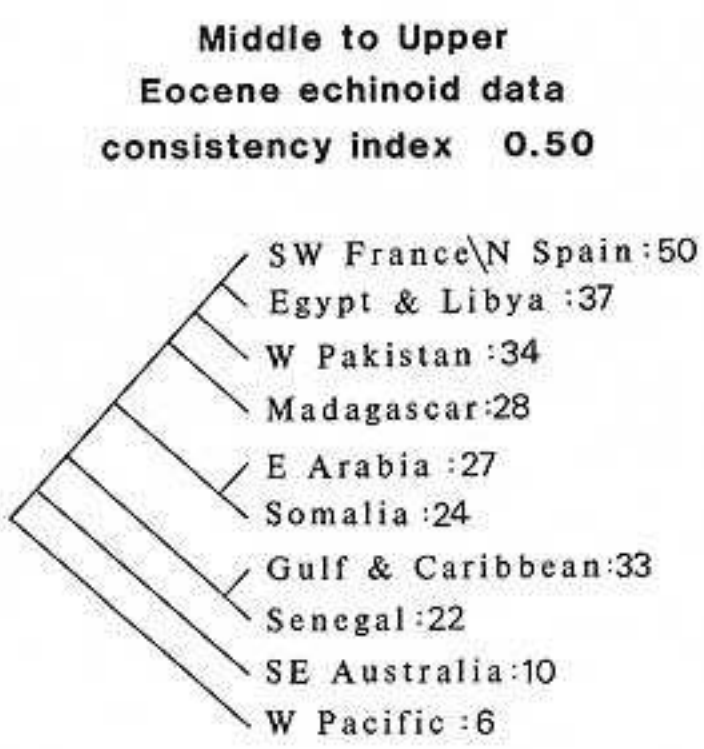

FIG. 5. Sample locality cladograms for Middle to Upper Eocene echinoids. The two alternatives shown are equally parsimonious. Significance of numbers after localities is as for Fig. 3.

Upper Cretaceous (Campanian/Maastrichtian data) (Fig. 6)

Our data for Campanian/Maastrichtian echinoids gave four equally parsimonious cladograms, with the lowest consistency (0.42) so far. This low consistency is largely a result of the ambivalent position of the paired regions, north-east Arabia and southern Iran, the program offering two alternative relationships; one linking it to Asia (Baluchistan plus South Tibet), the other with the Atlantic/Europe/Indian Ocean group. Neither Baluchistan (the Mari Hills) nor South Tibet (south of the Zangbo suture line) is well monographed, and they may therefore appear 'primitive' through pseudo-absences. (Indeed, examination of the Tibetan fauna by A. B. Smith since we analysed the present data has revealed a number of taxonomic errors.) The major ambiguity resulting from this switching obscures almost any major pattern, though two geographical regions are consistent in themselves, namely an Atlantic/Mediterranean/Europe group and a north-east Arabia and Iran group.

The polychotomy prevents any inferences being drawn about relative timing, but as noted already, a similar intra-Atlantic event occurs

Historical biogeography

Historical biogeography is the study of the history of geographical distributions of organisms and of the historical factors which affect geographical distributions. Amongst its particular aims (see Patterson 1983 for a discussion), the one most relevant here is its use of patterns of distribution of living and fossil organisms to reconstruct geological history. Unfortunately, there are many historical factors that might affect the distribution of biotas and we should assume, neutrally, that these factors function on different scales of time and space to produce a spectrum of effects. Some may affect the geographical range of only a single species, whereas others, such as continental rifting or collision, isolation of oceanic basins, or global changes in climate or ocean circulation patterns, are historical factors which we might expect to affect large segments of the biota simultaneously. It follows that any method which uses distributions to infer history must be able to distinguish broad-scale events affecting most biotas (extrinsic events), from those which affected only small numbers of taxa.

Over the last decade, there has been considerable controversy about methodology in biogeography and about the factors which govern organic distributions (e.g. Nelson and Rosen 1981). There has been a resultant shift towards the use of analytical methods (Patterson 1983), and towards the recognition of factors other than dispersal and ecology (especially *vicariance*: the appearance of new species as a result of a new biogeographical barrier). There is however no method which establishes the causes of all distributions, and in any case, as we explain later, there are different questions which need to be answered.

Until this controversy arose, biogeographical patterns were interpreted largely in terms of centres of origin and dispersal patterns (but for a history of the subject, see Nelson and Platnick 1981, and Humphries and Parenti 1986). Historical biogeographers relied heavily on palaeontological data on fossil distributions to identify these centres of origin and the associated dispersal pathways through time (for examples, see Wiley 1981; and for a defence and exposition of this approach see Briggs 1984). With the advent of plate tectonics and theories of continental drift there has been a change in emphasis towards scenarios where extrinsic factors, especially plate tectonics, were seen as controlling biogeographical patterns, and the fossil record interpreted to fit in with the currently favoured tectonic model (e.g. in Hughes 1973). More recently still, the role of fossil data as the key to interpreting historical biogeography has come under serious attack, with claims that fossil data cannot add anything to our understanding of the Recent biogeographical distribution of the biota (for a review see Patterson 1981, and for a counter-argument see Ghiold and Hoffmann 1986). Centres of origin hypotheses and scenarios have been criticized as untestable (Nelson and Platnick 1981; Patterson 1981, 1983; Wiley 1981). Add to this the current debate as to whether dispersal or vicariance dominate in biogeographical processes (McCoy and Heck 1983), and it is easy to understand why historical biogeography is in a state of flux.

Fossils in historical biogeography

In view of the current criticisms of the use of fossils in historical biogeography, and the fact that we make use of them here, it is appropriate to include a brief discussion, concentrating on the use of fossils in presence/absence methods (rather than their palaeoenvironmental significance).

Primary biogeographical data consist of the presence or absence of taxa, but these are not necessarily comparable attributes. The presence of a taxon relies upon the competence of the taxonomist but is otherwise unambiguous. By contrast, the absence of a taxon is ambiguous for one of three possible reasons: the taxon may: (1) have never existed in the area (*primitive absence*); (2) exist in the area but may not yet have been recorded (*pseudo-absence*); (3) have existed in the area in the past but may have since become extinct (*reversal absence*). These concepts can also be applied to an entirely fossil biota, by taking the fossil horizon as the vantage point. The likelihood of pseudo-absences obviously diminishes as the biota of the region becomes better known, but is much more of a problem for palaeontological data than it is for Recent data, especially in the less well-studied areas of the world.

It is the problem of distinguishing pseudo-absences from primitive absences that has led some biogeographers to claim that fossil evidence cannot contradict the distributional pattern of modern biotas (namely Croizat 1964). Yet it is the recognition of reversal absences that has led non-vicariance biogeographers to believe that fossil data are important for our understanding of historical biogeography. Clearly though, fossil data can only extend

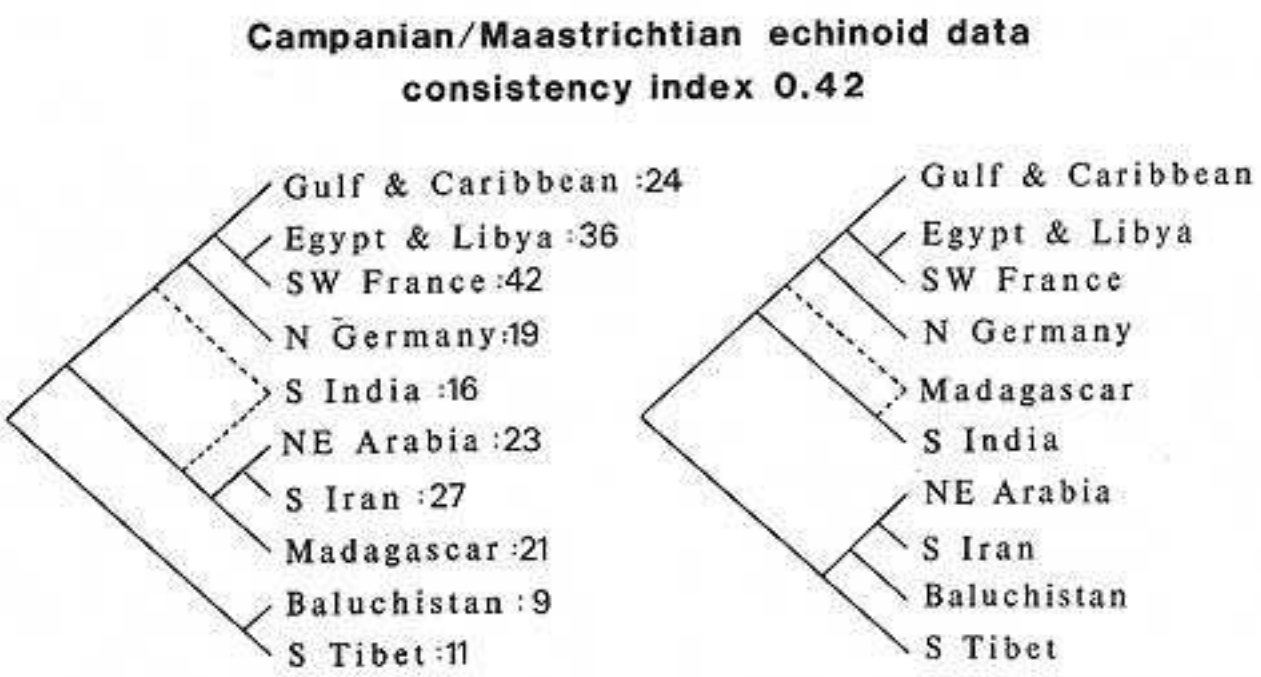

FIG. 6. Sample locality cladograms for Upper Cretaceous (Campanian–Maastrichtian) echinoids. The two cladograms shown are equally parsimonious, and each has two alternative positions for one locality (South India and Madagascar, respectively). Significance of numbers after localities is as for Fig. 3.

both here and in the Eocene data, and points to this being the most certain of the events suggested by the evidence so far. The Indo-Pakistan affinity with Madagascar is eye-catching, implying faunal exchange between these two now widely separated localities at some time earlier in the Cretaceous.

Upper Jurassic data

Our results, for corals alone, were disappointing and are not even reproducible, consisting of almost three hundred equally parsimonious alternative area cladograms! Consistency (0.295) was, not surprisingly, low, suggesting that either the data matrix was bad, due to poor taxonomy or inaccurate distributional information, or that the distributional pattern of corals in the late Jurassic was dominated by chance dispersal and/or convergence events, or a combination of these factors.

Discussion

Geological history?

So far, we have concentrated on inferring divergences and convergences, without further interpretation of these events in terms of geological history. Left like this, they represent a putative faunal history of what is usually regarded as the 'Tethyan' region (with Pacific). In this section we go on to compare some of the least uncertain of these inferred events with selected, independently derived, geological events. It is beyond the scope of this chapter to review all the existing literature on Tethys history that might bear on our own inferred events, so we leave readers, with knowledge or interests not discussed below, to make their own comparisons. We discussed the basis on which we make the comparisons on pp. 285–7.

Intra-Tethyan divergences in the Middle East region

The literature is widely in agreement that, for the time covered by our results, Tethys was largely a continuous marine region connecting the Atlantic to the Indian Ocean until final closure in the Miocene, though opinions differ on final closure date within the Miocene. There is also frequent mention of the cosmopolitanism of Tethyan biotas in both the Mesozoic and Palaeogene. Yet our results show faunal divergence across the modern Middle East region in all four sets of cladograms, from the Campanian/Maastrichtian to the Recent. Does this represent one event or recurrence of divergences in more or less the same region?

We found preliminary evidence (above) for at least two events, both prior to the Oligocene. The similar pattern of divergence found in both of the later area cladograms could also represent further events, or simply be the continuing imprint of the earlier divergences through the rest of the Cainozoic. If so, it would amount to saying that the modern differentiation of faunas (at generic level) on each side of the Middle East

region goes back, not to the Miocene, as is widely stated (e.g. for corals, Wells 1956), but to some time in the Palaeogene or even late Cretaceous. This was actually implicit in the analysis of the stratigraphic ages of extant reef coral faunas by Stehli and Wells (1971) and B. R. Rosen (1984), who showed that living Atlantic reef-coral genera are predominantly Cretaceous to Palaeogene in age. In other words, although the modern Indo-Pacific and Atlantic came into being as *physical* entities during the Miocene (by almost universal agreement), the marine *biotas* on either side of the Middle East had become differentiated at generic level a long time before the Miocene. It seems that final closure of the Middle East (itself a modern observable fact) affected shallow-marine organisms principally at species level (e.g. Adams *et al.* 1983) and was not detectable by our analysis.

An alternative possibility is that the Middle East emergence is older than the Miocene age generally attributed to it. Certainly, the precise age of final closure is not widely agreed as yet, so it may be of interest to briefly consider independently derived histories of this region. Taking the pre-Miocene first, Adams (1981) mentions the possibility of a marine regression which left a dry land-bridge area across the Middle-Eastern Tethys in the Palaeocene (Danian), and this might correspond with the later of our two inferred events, as seen in the Eocene results. Adams also mentions a similar event that may have taken place in the Oligocene, and so the divergence seen in our early Miocene results may be this Oligocene event, not the continued imprint of the Danian one. For the Miocene closure of Tethys ('the terminal Tethyan event'), Adams *et al.* (1983) believe that this occurred in the early Miocene (mid-Burdigalian), and other authors (e.g. Schafersman and Frost 1979; Ali 1983) have also suggested a variety of early Miocene dates. Rögl and Steininger (1983, 1984), however, believe that final closure had occurred by 11 to 12 Ma (early Tortonian–Pannonian–late Bessarabian) in the late Miocene, with periods of evaporite deposition and shoaling in the Middle East seaways, at various times between the late Oligocene and late Miocene.

Unfortunately, our data lack the resolution necessary to decide between these competing hypotheses, and any number of events can be hypothesized between our sample horizons. The resolution of biogeographical data could be increased by using lower taxonomic groupings (species rather than genera) and more numerous sample horizons of shorter duration (stages rather than groups of stages). In this way, consecutive identical area cladograms could be taken as evidence of continuing divergence and isolation of faunas, whereas alternate clustering and divergence through time would provide proof of multiple vicariance events. (We chose our taxonomic level and sample horizons to investigate global changes in biotic distributions, showing that it is important to choose a level of taxon and geological time that will be relevant to the question in hand.)

In summary, our present results do not test how many vicariance and convergence events there were in the late Mesozoic to Cainozoic history of the Middle East, but we can state that there has been a longer history of Atlantic/Indian Ocean faunal differentiation than has usually been recognized, and this extended back to the Cretaceous. From the limited resolution gained in our study, there is evidence for at least two and probably three such vicariance events. Faunal divergence is not all due to final closure in the Miocene. Too much emphasis has been placed on the presumed effect of final closure on biotas, though we recognize the converse value of detailed taxonomic evidence at species level for mapping and dating this event.

Isolation of the Pacific faunas until the Neogene

According to Schlanger and Premoli-Silva (1981), there was large-scale volcanicity and uplift in the mid-Pacific during the Cretaceous, and this coincided with, and probably caused, a faunal convergence of the Mid-Pacific with the Caribbean. Their suggestion implies that the Mid-Pacific must previously have been cut off, not only eastwards towards the Caribbean, but also westwards, otherwise, the Earth being round, Caribbean faunas could have been in exchange with the mid-Pacific via other directions than the East Pacific. Unfortunately, we have no relevant late Cretaceous data to compare with Schlanger and Premoli-Silva's suggestion, but our Eocene results do suggest that at some time before or during the Upper Eocene, the Mid-Pacific was in faunal interchange with other regions, although we cannot say in which direction.

Schlanger and Premoli-Silva observe that later, 'by the Tertiary', the Mid-Pacific faunal interchange with the Caribbean was disrupted and convergence occurred instead with faunas to the west (i.e. eastern Tethys and the Indian Ocean). Our results do not contradict this, so long as this western convergence was Eocene or earlier. But, in addition, they also suggest that by a later date (no later than the end of the

Eocene), there must also have been a divergence event or events which isolated those parts of the Pacific (i.e. those actually sampled by us) in all directions. In fact, it is simpler to infer a single event of simultaneous convergence to both east and west of the mid-Pacific in the Cretaceous from our results (as discussed by Kay 1980, 1984), rather than a sequence of switched convergences, as suggested by Schlanger and Premoli-Silva, and for which there is, as yet, no evidence. This event was then followed by divergence, and isolation by no later than the end of the Eocene.

The nature of the barriers that were involved in this Pacific history must remain, on present evidence, speculative. The present form of the Pacific basin makes it difficult, however, to imagine how there could have been any land barriers across its tropical part, in the time span covered by our study, so it seems that sheer isolation of island localities must have been important. In other words, we envisage that any barriers that might have existed in the Pacific consisted of great oceanic expanses, without intermediate islands, and that it was distance, possibly coupled with oceanographic factors, that limited the geographical ranges of shallow-marine benthic organisms. The East Pacific today is usually regarded in this way.

Conversely, the breakdown of these oceanic barriers could arise from changes in oceanography or the emergence of islands and landmasses in previously empty regions, or both. These would have had a 'staging post' role (B. R. Rosen 1983, 1984) for previously confined biotas, providing them with habitats in places where no suitable habitats existed before, and so allowing them to expand their ranges into previously unoccupied regions. ('Staging posts', a dispersion concept, may also have acted as stepping-stones, a dispersal concept, but, by definition, the reverse cannot be true.) The speculative explanation for mid-Pacific biotic convergence, advanced by Schlanger and Premoli-Silva (1981) and widely cited by others, is that a significant land area or dense archipelago emerged in the Mid-Pacific, as a result of large-scale Cretaceous volcanicity, and this effected *eastward convergence* of biotas, while its later subsidence brought about their *eastward isolation and divergence*. Whatever TECO model is adopted for explaining the biotic events, our limited data suggest that a Cretaceous or earlier phase of faunal intermixing was followed by isolation and divergence in the Pacific, in effect by the middle Eocene, and this is compatible with Schlanger and Premoli-Silva's hypothesis.

This isolation of the mid-Pacific continued until the *westward convergence* in the post-Lower Miocene resulted in the appearance of an Indo-Pacific fauna (as distinct from the previously different Indian and Pacific Ocean faunas). The most likely factors which brought isolation to an end are the northward movement of Australia towards south-east Asia, and the associated uplift of additional island masses in the West Pacific, like Papua New Guinea. These regions would have had a 'staging post' role between the Indian Ocean (and Indonesia) and the Mid-Pacific. Audley-Charles (1981) gives a later-early Miocene date for the start of collision between Australia and south-east Asia, and this fits well with the post-early Miocene date of West Pacific convergence, inferred from our own results. In addition, the westward movement of islands on the Pacific Plate could also have caused a convergence of biotas at Mid-Pacific localities with those west of the western plate boundary, but this is beyond the resolution of our study.

Finally, it is also of note that in Springer's (1981, 1982) cladistic biogeography of Recent shore fishes of the Pacific, he concluded that the Western Pacific plate boundary was a consistent vicariance line. Nelson (1985) in his remarks on the cladistic biogeography of anchovies notes a divergence between the 'West Central Pacific' and the 'Indo-West Pacific' which may also represent the same event. These observations could be explained by the same pre-Oligocene divergence inferred here, which isolated the biotas on the Mid-Pacific islands from those around the landmasses to the west. These landmasses would have been concentrated west of the plate boundary (on today's evidence), due, in part, to subduction zone activity. Continuing plate collision, and associated loss of crust between the West and Mid-Pacific since that time, would mask the degree of physical isolation of the Mid-Pacific as it might have been in the pre-Oligocene (though it should be possible to estimate it).

In general, our results corroborate Kay's (1980, 1984) synthesis of the history of the Pacific marine biota, except that our evidence for a western convergence indicates a post-Lower Miocene rather than an Upper Eocene event.

Eastern Pacific

Complementary to the Mid-Pacific isolation in the Palaeogene, there is, today, still a major oceanic barrier between the Mid-Pacific and the Americas. Most authors believe that this barrier

is at least as old as the Lower Miocene and, as discussed in the previous section, it may go back through most of the Palaeogene. Since the Miocene, echinoid faunas on the Pacific coastline of the Americas, as well as in the Galapagos and other Eastern Pacific islands, have had the Atlantic fauna as a sister group (prior to this we have no relevant data). The same kind of pattern is well established for numerous organisms, the general explanation being that the seaways between the Caribbean and Pacific remained open until the formation of the Isthmus of Panama in the Pliocene, maintaining faunal exchange between the two areas, while the Eastern Pacific oceanic barrier prevented exchange westward with the rest of the Pacific.

Our data on reef corals, however, prove an exception to this pattern. Dr. Nancy Foster (pers. comm.) states that there are Pliocene corals in the western coast region of the Americas with Caribbean affinities (not included in our samples), suggesting that corals at that time had the same pattern of distribution as other groups. It seems highly unlikely that selective extinction of those corals with Caribbean affinities has taken place, leaving only those with old Pacific affinities. More likely, in our opinion, is that Eastern Pacific corals have suffered a major extinction event after the closure of the Panama seaway, and that what we now see is the colonization of the Eastern Pacific by elements of the Indo-Pacific corals, producing a late Cainozoic trans-Pacific convergence. Heck and McCoy (1978), however, prefer the idea that the corals concerned must have continued to exist in populations not found in the fossil record of the Eastern Pacific. Our method does not resolve these alternative arguments, but their hypothesis is as open to the criticisms of special these alternative arguments, but their hypothesis is as open to the criticisms of special pleading and untestability as they say long-distance dispersal is.

Present distribution

Our results support Kay's (1980, 1984) conclusions that the present patterns of endemicity and cosmopolitanism in shallow-marine biotas reflect a long history of fragmentation and divergence since the Cretaceous, especially for the Pacific, but we would add that Tethyan faunas themselves were not cosmopolitan during much, if any, of this time, even during the Cretaceous. This can be deduced from the intra-Tethyan divergences identified throughout the span of our study. It is clearly an oversimplification to regard modern biotas as having derived from a 'previously widespread pan-Tethyean [*sic*] biota' of Cretaceous age (e.g. McCoy and Heck 1976; Heck and McCoy 1978).

Older ideas of an Indo-West Pacific centre of origin for Indo-Pacific biotas, or even worldwide biotas (e.g. Stehli and Wells 1971) remain difficult to assess, and many authors have pointed out that such an hypothesis is indeed untestable (see p. 276). The centre of origin model is not, and cannot ever be, contradicted by any results using distributional data such as our own. The Indo-West Pacific might as easily have been a 'centre of *refuge*', since our results imply that it is also the only region whose biotas have intermixed with all other Indo-Pacific localities, since some time before the end of the Lower Miocene. It is certainly hard to understand why, if assuming allopatric speciation, a dense pattern of islands should have been a more important source of new species than the more scattered pattern of islands further out in the Indian and Pacific Oceans. A centre of origin model seemingly implies a high level of sympatric or non-geographical allopatric speciation within this Indo-Pacific 'centre'. (For a more detailed 'vicariance and refuge model' for the Indo-Pacific, see B. R. Rosen 1984, 1985, and for a discussion of this and two other historical hypotheses, see Potts (1985)). It is too early to specify events, but PAE results offer a way of testing these various models. First results do show post-early Miocene intra-Indo-Pacific divergences, some of which only make sense if they were preceded by an intra-Indo-Pacific convergence, consistent with Rosen's model.

Conclusions

Parsimony analysis of shared presences provides data on the relative recency of faunal contact between regions, from which it is possible to deduce a history of extrinsic divergent and convergent events. These cannot provide definitive palaeogeographies by themselves, but yield empirical constraints on reconstructions based on independent evidence. This is because barriers to faunal exchange do not need to be physical structures, and there is no way of deducing the nature of a barrier from the faunal distribution pattern alone. The addition of ecological inferences would assist in the process of reconstructing palaeogeographies, but introduces assumptions (i.e. about the modes of life, dispersion capability, and preferred habitat of fossils) at the possible expense of rigour. Biogeographical data can be compared with

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independent lines of evidence, such as that derived from facies interpretation, to assess palaeogeographical reconstructions.

Such comparisons between parsimony analyses of biotic distributions and palaeogeographies would, in the long term, be more useful in the earliest Mesozoic and in the Palaeozoic, than for the time since then—where we have a much greater wealth of independent geological data (e.g. magnetic lineations). Older palaeogeographical reconstructions are more conjectural, and the constraints provided by biogeographical analysis should therefore have proportionally greater value, as we go back in time.

Essentially, though the palaeogeographical role of biogeographical analysis is inevitably 'narrative' (Ball 1976), a clear distinction ought to be maintained between analysis, test, comparison, and self-consistent explanation. As Patterson (1983) points out, even narrative approaches need a method, and we would claim that parsimony analysis of shared presences, like cladistic biogeography, does at least provide 'a methodology for capturing the pattern' (Eldredge 1981). Even cladistic biogeography can only be compared with independent palaeogeography on a narrative basis. Neither method, however, is in itself narrative, in that they both provide hypotheses about the history of areas in terms of their characteristic biotas, that are rigorous and testable on the criterion of congruence. Ideally, this congruence would be between different taxonomic groups, between the results obtained from both methods, and between data sets from sufficiently closely spaced stratigraphic horizons. We therefore offer our inferences, not so much for their present value as definitive accounts of Tethyan history, but as the first steps towards a testable history of Tethyan marine biotas which is independent of other data. If few of our historical conclusions are especially new or revolutionary, we hope, at least, that we have demonstrated the potential of this kind of biogeographical analysis. We anticipate a refinement of the method and new findings based on it, in the future.

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Appendix: Sources of distributional data

Echinoids

Recent

See main text (p. 289 and Acknowledgements).

Lower Miocene

Gulf and Caribbean	Kier 1984 (Cuba); Jackson and Vaughan 1922 (West Indies); Cooke 1959 (south-east United States of America), Poddubiuk and Rose 1985 (Antigua and Anguilla)
Mediterranean	Caria 1975 (Sardinia); Rose 1974 (Cyrenaica, Libya); Rose 1975 (Malta); Negretti 1985 (south-east France, Alpes Maritimes)
Saudi Arabia	(Dam Formation) Clegg 1933 (Bahrain Gulf), Kier 1972 (Riyadh, Saudi Arabia); Roman 1976 (Qatar)
Madagascar	Cottreau and Collignon 1927 (south-west part)
West Pakistan	(Gaj Series) Duncan and Sladen 1885 (Sind)
Indonesia	Jeannet and Martin 1937 (Java)
Japan	Nisiyama 1966, 1968
SE Australia	Clark 1946; Philip 1963, 1964, 1965, 1967, 1969, 1971; Philip and Foster 1971; McNamara 1985*a*,*b*; McNamara and Philip 1980*a*,*b*, 1984
New Zealand	Fell 1954; Henderson 1975
Mid-Pacific	Kier 1964 (Marshall Islands); Cooke 1957 (Saipan, Mariana Islands); Nisiyama 1966, 1968

Middle–Upper Eocene

Gulf and Caribbean	Cooke 1959 (south-eastern USA); Kier 1980 (North and South Carolina); Kier 1966 (Barbados); Kier 1984 (Cuba); Jackson and Vaughan 1922 (West Indies)
Spain and south-west France	Lambert 1927, 1928, 1933 (Barcelona and Catalonia); Castex and Lambert 1920; Castex 1930, 1947 (south-west France, Biarritz)
North Africa	Lambert 1931
Senegal	Roman and Gordinski 1959
NE Arabia	(Dammam Formation) Roman 1976 (Qatar); A. B. Smith's own data (north-east Oman)
Somalia	Kier 1957
Madagascar	Lambert 1929, 1933, 1936*a*,*b*
NW Pakistan	(Khirthar Series) Duncan and Sladen 1884
SE Australia	Clark 1946; Philip 1963, 1964, 1965, 1967, 1969, 1971; Philip and Foster

	1971, McNamara 1985*a*,*b*; McNamara and Philip 1980*a*,*b*, 1984

Campanian/Maastrichtian

Gulf and Caribbean	Cooke 1953, 1955 (south-eastern USA); Kier 1984 (Cuba), Jackson and Vaughan 1922 (West Indies)
NW Europe	Schlüter 1883, 1892; Ernst 1972
N Africa	Lambert 1931; Petitot 1961 (Morocco)
Saudi Arabia	Aruma Formation, Kier 1972
Oman	A. B. Smith's own data
Madagascar	Lambert 1933*a*,*b*, 1936*a*,*b*; Cottreau 1935
Iran	Cotteau and Gauthier 1895 (Louristan)
Baluchistan	Noetling 1897 (Mari Hills)
S Tibet	Wu and Mu 1976 (south of the Indus Zangbo suture)
S India	Stoliczka 1873 (Trichinopoly and South Arcot)

Reef-coral data

Recent

See text (p. 289 and Acknowledgements)

Lower Miocene

The stratigraphic correlation of particular strata at some of these localities has been reinterpreted in the light of more recent literature and also on the advice of Dr C. G. Adams (Department of Palaeontology, British Museum, Natural History), for which we thank him. We also thank Dr S. H. Frost (now of Gulf Research and Development Co.) for making available to us his unpublished compilations (as of 1981). B. R. Rosen is responsible for the taxonomic reinterpretation of various records.

Gulf and Caribbean	Frost 1977; Frost 1981 (unpublished compilations)
Mediterranean	Frost 1977, incorporating Chevalier 1962; Frost 1981 (unpublished compilations)
Iran	Kühn 1933; Sjerp *et al.* 1969 (Saidabad area); Rosen and Darrell in press (Makran)
West Pakistan	(Gaj Series) Duncan 1880 (Sind)
Indonesia	Felix 1921; Gerth 1921, 1933; Gerth 1923 (Borneo); Umbgrove 1943 (Sumba); Osberger 1954, 1955*a*, 1955*b* (Java). See also Indonesia compilations by Gerth 1925, 1931, and Osberger 1956
New Zealand	Hayward 1977
Marshall Islands	Wells 1954, 1964

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the total geographical range of a taxon, since the ambiguity of absence precludes using absence data to identify patterns of range shifts. Adding to the geographical range of a taxon does little to clarify area relationships and often simply reduces the level of resolution of the study.

The usefulness of fossil data, and the way in which fossils are treated, depends upon the sort of information being sought. For workers interested in the historical biogeography of a group with an excellent fossil record and its distributional history, it is probably valuable to use fossil distributions to identify possible changes through time, always bearing in mind the ambiguity associated with absence of taxa. This approach must always remain narrative and speculative and cannot be used as a test of past palaeogeographies. For workers interested in the historical background that produced modern patterns of distribution, the distribution of living biotas is a much less ambiguous guide which cannot be contradicted by fossil discoveries (D. E. Rosen 1978; Humphries and Parenti 1986).

However, in this paper we are neither interested in reconstructing the historical development of a specific clade, nor in confining ourselves to the particular origins of the distribution pattern of the present-day biota. Our aim is to recognize past patterns of organic distribution and their relevance to testing palaeogeographical reconstructions. This cannot be done without data on the distribution of fossils, especially in the earlier Phanerozoic (see also Young's (1981) discussion, pp. 232–3). Data from living distributions alone are insufficient because, although the geographical distribution of the Recent biota is in part the product of a long and continuous sequence of extrinsic factors that stretches back well into the Precambrian, it must reflect events in the recent past much more strongly than older events. The influence of older events may also be apparent in a Recent distributional pattern, particularly at higher taxonomic levels, but they must have a weaker imprint because more recent events have masked them. We base this view on two factors: (1) *convergence*; and (2) *evolutionary development*, best explained in terms of a descriptive model.

Convergence of biotas results from events like continental collisions (e.g. for terrestrial and shore organisms) or continental rifting (which, for example opens connecting seaways for marine organisms) and therefore overprints previous distribution patterns. Continued evolutionary development of a biota, with the appearance of new sister taxa and the extinction of established taxa, continually creates new biotas, and these must be restricted in their distribution by whatever biogeographical barriers existed at the time. We therefore assume that for heuristic purposes, distributional patterns are at least in part a response, direct or indirect, to geological events. (Why else try to use distributions to infer geological history?) Moreover, with respect to any given time plane, as older taxa which were penecontemporaneous with older events become extinct, and new ones arise reflecting more recent geographical patterns, the older distributional patterns will become less and less distinct. For this reason, we believe that the resolution of historical events using only extant biotas must deteriorate with the geological age of these events, and a Recent distribution (for example) will be much less reliable in assessing pre-Cainozoic, or possibly even Palaeogene, than Neogene palaeogeography. One obvious way to recover this lost information is to choose one or more additional observation datum planes in the geological past, and look for patterns in, say, the Oligocene, or Silurian. We develop this approach further here.

Superimposed on this pattern of diminishing information content, there will also be differences between major taxonomic groups because they have apparently different average species durations (approximately 6 Ma for echinoids, according to Stanley (1979), and 10–15 Ma for reef corals according to Dr A. B. Foster (pers. comm.) and hence, presumably, different average generic durations. The rate at which past extrinsic events will be removed from the biogeographical distribution record will therefore vary from group to group. If corals last on average twice the duration of echinoid species, then the biogeographical pattern of corals will be expected to retain evidence of previous extrinsic events for comparably longer than that of echinoids, while the echinoid pattern will reflect recently past events much more strongly than the coral pattern.

We agree with the common criticism that the incompleteness of the fossil record raises serious difficulties for biogeographical methodology, but it is a reasonable goal to try to find ways of making the best biogeographical use of this record rather than rejecting it outright. How should we do this? Simply to combine Recent and fossil data, effectively superimposes and amalgamates potentially interesting signals from different geological horizons and loses potential stratigraphic resolution (Grande's (1985) 'point 4', p. 236). We therefore assume that, at any given horizon, the fossil record is a vestigial

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biogeographical sample from which it is still possible to infer historical events, however incompletely, according to explicit, rational methods. Fossil distributional data clearly have an important role in historical biogeography, *if* they are analysed using a method that (1) minimizes the problems associated with absence states; and (2) is based on separate analyses of biogeographical distributions from different, preferably successive, geological horizons. The distribution for each such horizon should have a pattern that most strongly reflects the major biogeographical events that have taken place over the most recent time span prior to that horizon. This approach could be applied to cladistic biogeography, for example, by taking phylogenies of different groups of taxa within a past time-plane, or, synoptically, over a stratigraphic sequence, rather than using Recent biotas alone (B. R. Rosen 1984, and for an example, see Grande 1985). It is a synoptic (though not phylogenetic) approach that we have also adopted here.

Some current methods of analysing distributional data

Importance of endemicity

Biogeographers are universally agreed that endemicity (the exclusive occurrence of a taxon in a particular locality or region) is the most significant feature of distribution patterns. In the simplest instance, every region would have its own exclusive biota without any overlap with other regions, but in practice, even for small taxonomic groups or small areas, this is rarely if ever the case. Endemicity, moreover, is relative, and this is for two reasons. Firstly, in biogeographical practice, distributions (including areas of endemicity) are invariably generalized to a greater or lesser extent; they are syntheses of the raw distributional data gathered from an original set of sample points (Nelson and Platnick 1981). Secondly, a taxon which is shared between two given regions, but which occurs nowhere else, is 'endemic' to both regions when considered together, but 'endemic' to neither when each area is considered separately. Thus for sampling purposes, the biosphere must be assumed to consist of an overlapping mosaic of endemicities or ranges of different species (B. R. Rosen 1984). As we explain below, this overlap has always made delineation of biotas and regions difficult, but it can actually be used to make hierarchical groupings of sample localities.

The way in which distributional data are analysed is crucial to how they can be interpreted, and the following is a critical summary of some of the main methods that are in current use.

Anecdotal treatments

Unfortunately, in many cases, extravagant claims about displaced (allochthonous) terranes and palaeogeography are based on the discovery of one or a few taxa common to two or more regions, without considering the biotas of the regions as a whole. Such shared taxa may reflect similar prevailing ecological conditions in the two areas, rather than any extrinsic (e.g. tectonic) factor. They could even represent disjunct remnant isolates of a previously more extensive range. Such claims are limited in merit and are best treated as preliminary hypotheses.

Biotic provinces

Provinces are not in themselves a method, but rather are a conceptualization about the nature of biotic distributions. There is a long-established history of the use of this concept, going back to Sclater, de Candolle and Wallace (Nelson and Platnick 1981). Provinces have played an important part in the history of the subject because they represent the discovery of the importance of endemicity, and the origin of the idea of relationships between regions.

Provinces are primarily a means of summarizing or generalizing endemic patterns, often by reference to 'key' taxa. Belief in provinces as a real phenomenon has generated a whole gamut of methods which are designed to find them (see below), but the idea meets difficulties with the overlapping nature of endemicity. Notwithstanding this overlap, provinces are invariably conceived as one- or two-tier divisions of the Earth's surface (e.g. Schopf 1979), rather than hierarchically. A common consequence is that studies based on different groups of organisms lead to rival, or apparently unreconcilable, schemes of provinces. For a fossil example, see Fortey and Barnes (1977), Cocks and Fortey (1982), and Schallreuter and Siveter (1985) on trilobites and brachiopods versus ostracods and conodonts in the Ordovician–Silurian.

The boundaries of many provinces, moreover, are defined, like those of Wallace, on mixed criteria, usually a combination of the distribution of certain organisms, and physical features like the present shoreline limits of a

continent. This hybrid approach is even more unsatisfactory when we come to fossil distributions. If, as is common, the geographical frame of reference for fossil distributional data is a palaeogeographical reconstruction, physical criteria for province boundaries must, inevitably, be more hypothetical than real (e.g. Tethyan Realm). How might we discover palaeogeography from fossil provinces which are defined in terms of what we are trying to discover? Even those provinces that are defined on the presence/absence pattern of organisms alone (see below) are subjective and arbitrary because of the problem of overlapping endemicities. We reject the idea that objective biogeographical provinces can be identified, and we prefer methods which use the relationships between sample localities alone to develop historical hypotheses.

Range analysis

Range analysis consists of superimposition of a set of organisms' distribution ranges, usually in two dimensions along a geographical sample line. Jablonski *et al.* (1985) stress that species' ranges are a fundamental biological unit, because ends of ranges have an ecological and evolutionary significance. Integration of range end-points can be used to delineate provinces, either in a simple visual way (e.g. Rosen 1984), or by statistical processing of range data (e.g. Pielou 1977, 1978; Jablonski and Valentine 1981).

As with phenetic methods (see below), geographical resolution of range methods is good, being potentially as fine as the set of sample localities. Range methods also answer some of our foregoing criticisms of provinces, in that range-defined provinces are based only on presence/absence data. Being essentially statistical, however, range methods are in fact phenetic and suffer from the same disadvantages. In particular, there is an arbitrary element (e.g. in deciding how many coincident end-points define a provincial limit). There is also the strong likelihood that in the pairs of provinces (regions) delineated by each peak of end-points, one of a pair might be defined on *absence* of taxa (cf. the problem of paraphyly in phylogenetics). These difficulties are more severe for fossil distributions, because of higher probability of pseudo-absences.

There is however a more obvious problem with range methods, because sample localities of range data are (by definition) fixed with respect to each other and a known geography, i.e. they are fixed to a geographical template. There are two consequences. Firstly, for fossil distributions, the only non-hypothetical geography which can be used objectively is the present Earth, but to plot the data on palaeogeographical reconstructions invites circularity. Secondly, for living marine and most fossil distributions, problems also arise if ranges are interpolated through points of absence between neighbouring records. (Some interpolation is usual because the same taxon is rarely present at more than a scatter of localities.) In fact, for distributions on a global scale, there is no way of deciding whether a range should be drawn along the shortest segment of the Earth's surface, or along the complementary longer segment. B. R. Rosen and Darrell (1984) could only devise arbitrary rules for interpolation.

These problems can only be solved by lifting sample localities off their geographical template altogether, as in other phenetic treatments like multivariate analysis, cladistic biogeography, and our own method of parsimony analysis of endemicity. Localities can then be grouped entirely on presence/absence, independently of any existing arrangement of these localities in space. (Parsimony analysis may itself interpolate records, but not according to neighbourhood considerations in a prior geographical scheme.)

Jablonski *et al.* (1985) also noted that ranges occur in overlapping sets, which therefore lend themselves to 'hierarchical analysis', but cited no examples or details. B. R. Rosen's (1984) method represents a simple hierarchical analysis, and our new method here is also a further development of this idea.

Similarity coefficients and multivariate cluster analyses (phenetics)

Rigorous treatment of biogeographical data has generally been based on some form of computerized multivariate analysis program (e.g. Stehli and Wells 1971; Whittington and Hughes 1972) which clusters pairwise calculations of similarity (or dissimilarity) calculated for biotas from a set of localities. Some authors have used similarity measures alone without clustering (e.g. Oliver and Pedder 1979). All these kinds of methods appear to give an objective assessment of biogeographical pattern. They are useful for recognizing areas of endemicity, and in defining provinces in the form of discrete clusters of sample localities. Some valuable features are that these methods can be used for a set of sample localities, without further prejudgement of how these localities correspond with regions

or provinces, and no interpolation of ranges is necessary. The methods are explicit, and locality control is as precise as wished.

However, there are many different similarity indices (Cheetham and Hazel 1969; Pielou 1979) and they can yield different results. The concept of similarity, moreover, is questionable. Most calculations use overall similarity, and this has been heavily criticized. (For a summary of criticisms of these techniques as applied to systematics, see Wiley 1981.) Another problem is that small but possibly significant endemic distributions can be lost as 'noise' (Nelson and Platnick 1981; Patterson 1983; and for a coral example, see B. R. Rosen 1984, p. 250). Although the methods themselves are explicit and strict, the choice of discriminant levels for clusters is subjective or arbitrary. Nonetheless, cluster analyses are a useful first step in defining cohesive regions, and clusters can be further evaluated by discriminant analysis (e.g. in systematics, Foster 1984).

Although cluster analysis produces dendrograms which could be taken to reflect a hierarchical pattern of provinciality, most authors usually choose to reduce them to the customary single-tier concept of provinces (e.g. Stehli and Wells 1971, for Recent reef corals). Provinces defined by similarity indices can be interpreted statically to indicate the contemporaneous presence and relative position of (unspecifiable) biogeographical barriers which can then be compared with palaeogeographical reconstructions based on other independent evidence. There is, however, no generally established method by which a cluster analysis, on its own, can be interpreted as a history of the evolution of taxa, biotas, or regions. In systematics, for example, there is no evolutionary theory by which overall similarity of characters in different taxa can be equated with similarity due to phylogeny, unless it is assumed that (1) rates of evolution for all the taxa concerned are the same, and (2) there has been no convergence of characters. (Dr C. J. Humphries, pers. comm.). Events are usually inferred from changing patterns of clusters (or cluster-based provinces) obtained from a sequence of stratigraphic horizons (i.e. a synoptic or stratophenetic approach, as used by Whittington and Hughes, 1972).

Cladistic biogeography

This is a relatively new development which has generated much of the recent controversy in biogeography (e.g. Nelson and Platnick 1981; Nelson and Rosen 1981). There are several methods that are related to this approach, but it is cladistic biogeography that offers a philosophically sound method for the historical analysis of distributions. The method deals only with clades of proven monophyly, whose relationships have been rigorously determined using cladistic methodology (i.e. there must be a well-corroborated cladogram of the group). On this cladogram, the geographical range of each terminal taxon is substituted for the taxon's name, and a hierarchical pattern of areas is worked out using simple principles (see Platnick and Nelson 1978; D. E. Rosen 1978; Nelson and Platnick 1981; Patterson 1981; Wiley 1981; Humphries and Parenti 1986).

This method produces, for each clade, a definitive hierarchical nesting of areas directly interpretable in terms of the group's historical biogeography. Furthermore, although it assumes that evolution occurs, it is otherwise independent of any theory as to how the pattern originated. The method is based primarily on presences alone, and identifies a branching phylogenetic pattern in a chosen taxonomic group. This, in turn, is taken to imply a history of vicariance events (the splitting up of previously unified areas, with contemporaneous divergence of taxa). Vicariance is assumed not on doctrinaire grounds (as is widely misunderstood), but as a falsifiable hypothesis. Where the vicariance pattern does not stand up to testing, other unspecifiable non-vicariant events (which might include dispersal or convergence) are inferred. Testing consists of comparing a number of such cladograms of different monophyletic groups, in a search for distribution patterns that are congruent. Congruence is taken to be evidence for large-scale extrinsic events, reconstructing palaeogeographies, or identifying divergences of biotas. Convergence of areas is inferred from synthesis of studies of numerous groups (Craw 1982; Humphries and Parenti 1986).

The main drawback of this excellent method is that it can only be used on proven monophyletic clades, and the state of taxonomy in many (especially extinct) groups therefore precludes its use. The method has mostly been used by biogeographers concerned with living biotas and, as far as we are aware, the only authors to have applied it to entirely fossil distributions are Young (1981, 1984) for Devonian fishes, Milner and Norman (1984) for Jurassic–Cretaceous ornithischian dinosaurs, and Grande (1985) for Eocene teleost fishes. There is no reason why it should not be attempted more widely by palaeontologists, although pseudo-absences are likely to be a problem.

A new method: parsimony analysis of endemicity (PAE)

Background and summary

From the foregoing discussion, it is possible to summarize some key criteria for achieving more rigour in historical biogeography, with particular respect to palaeogeography (Table 1). These criteria were a guide in developing the method used in this paper, though we have not necessarily met the criteria in full. This new method was first suggested by one of us (B. R. Rosen 1984, p. 251) as a development of range analysis, and as an improved means of discovering and analysing endemic patterns (of present-day reef coral distribution). This involved an intermediate stage of inferring ranges, which was subjective, arbitrary, and tied to existing geography (see p. 279). In place of range methods, it is possible to use parsimony analysis of taxa shared between sample localities, or more briefly, parsimony analysis of endemicity (PAE) without reference to any particular geographical pattern of the localities themselves. One of us (B. R. Rosen 1985) published a preliminary attempt in the following year, but apart from this, the method is largely untried.

Like multivariate analysis, PAE takes as its starting point the presence/absence data for a set of sample localities and a particular group of organisms. This minimizes geographical prejudgement. Each taxon present at a sample locality is then treated analogously to a character in cladistic analysis in systematics. PAE therefore uses the same kind of locality/taxon matrix for its raw data, as is used by cluster analysis, but instead of handling presence/absence in terms of overall similarity, it uses parsimony analysis of shared presence of taxa to identify a nested hierarchical pattern, as in cladistics. In this method, therefore, shared presences (endemicities) are treated analogously to synapomorphies in systematics. The resulting cladograms of sample localities express relationships between biotas, as represented at these localities. For

TABLE 1. *Some criteria for more effective application of historical biogeography to palaeogeography, using fossil distributions*

1. Keep biogeographical data and inferences distinct and independent from other data, and also from palaeogeographical inferences from other data (i.e. distinguish inferred history of the organisms from Earth history).
2. Use a data base of PRESENCE/ABSENCE for taxa from sample localities.
3. Make explicit and minimize ecological assumptions about the organisms used in distributional analysis.
4. Make explicit and minimize geographical extrapolations from the sample localities.
5. Use non-polyphyletic taxa.
6. Minimize the effects of pseudo-absence by using methods which emphasize PRESENCE of taxa and which do not rely on range determinations.
7. Maximize fossil data by analysing distributions over as many stratigraphic horizons as possible (but see also 8.).
8. Use time spans between stratigraphic distributions which are less than the mean duration of the taxa concerned.
9. Use stratigraphically well-controlled distributions.
10. Use a method which provides a consistent and explicit means of inferring historical events (i.e. other than narrative).
11. *Use a testable method.
12. *Use a method which distinguishes small-scale random events from major events.

*The only satisfactory means of achieving these criteria is to use a method which can be repeated for numerous organisms, seeking congruence between them.

reasons explained more fully below, these relationships can, in turn, be read as histories of these biotas, or as histories of the sample localities (which may be generalized, subjectively, as areas). Corroboration of these historical hypotheses is found by searching for congruence in analyses of as many different groups of organisms as possible.

PAE cladograms therefore provide an alternative to the dendrograms of multivariate analysis, avoiding the difficulties of both overall similarity, and dependence on arbitrary decisions about levels of discrimination. They also provide a direct (hypothetical) indication of historical events (i.e. without necessarily using a synoptic approach). Like phenetic approaches, PAE has the advantage that it can be applied to groups whose phylogenetic relationships are unspecified and which need not be clades of proven monophyly. However, the individual taxa used as attributive characters of the sample localities should be, as far as possible, non-polyphyletic (which for the sake of the present paper, we have had to assume). Apart from this, PAE side-steps the lengthy task required by cladistic biogeography, of establishing fully corroborated phylogenies, before even commencing biogeographical analysis proper.

Interpretation: (1) biotic history

For this paper we have used Swofford's (1984) PAUP computer program (version 2.2) to find the most parsimonious hierarchical arrangement of sample localities. When applied to phylogenetics, this method requires that an outgroup taxon be chosen for comparison with the main set of taxa. This procedure is critical to the historical interpretation of cladograms. An outgroup is used to root the cladogram and polarize the character states. For a biogeographical analogy, we would need a locality characterized by a supposedly primitive biota, i.e. a 'centre' or area of origin. This might be possible for a small, well-defined clade with a good fossil record, but it is clearly ridiculous to attempt to identify an area of origin for major groups such as echinoids or reef corals. Moreover, choosing one sample locality as an outgroup prejudges the area relationships which we are trying to discover, and is not feasible for non-monophyletic groups.

To avoid these problems, we preferred to use the program's Lundberg rooting. In systematics, this would be a taxon without any of the characters which occur in the other taxa being analysed. In biogeographical terms, it represents a sample locality without any of the taxa which are present in the rest of the sample locality set. Such an outgroup might be thought of as a locality occurring so far back in geological time that none of the taxa in the sample set of localities had yet evolved. In this interpretation, as taxa appear, their distribution is restricted by prevailing biogeographical conditions, and the presence of shared taxa between two or more sample localities provides a historical dimension. The resulting cladogram of sample localities therefore represents not simply an analysis of shared presences, but also a hierarchical pattern that can be interpreted in terms of the evolution of biotas.

At this point, we should admit that other biogeographical interpretations of distributional patterns derived from the Lundberg rooting are also possible, such as relative effect of adverse ecological factors (e.g. extreme temperatures, high latitude), although there will still be a historical component in such circumstances. It is likely, therefore, that PAE using Lundberg rooting will pick out contemporaneous ecological gradients on a global or regional scale, as well as historical patterns. However, we rejected the alternative of using an outgroup area with all taxa present (which would yield an inverted version of the Lundberg-rooted cladogram), because the resulting pattern implies a history of congruent geographical depletion through time, starting from a cosmopolitan biota, and would group areas according to shared absences. Despite drawbacks, Lundberg rooting seems to be the most appropriate method, so far, for PAE purposes, and we have assumed that this rooting gives cladograms which can be interpreted as historical biogeographical schemes of sample locality relationships, intermingled with some ecological influences.

In a purely historical interpretation, each dichotomy in a PAE cladogram represents a biogeographical divergence of at least one pair of taxa, or more (hence biotas), between the sample localities under analysis. A complete cladogram provides a sequence of such events, in which dichotomies nearer to the origin of the cladogram represent older divergences than those further from the origin. This does not rule out the possibility of convergences also having occurred, but these cannot be read directly from the cladogram itself (see below). A hierarchical pattern of distribution exists because of the history of divergences which have fragmented the biota: convergence acts to destroy this pattern by merging the biotas represented at sample localities.

Since an ecological interpretation cannot also be ruled out, a PAE cladogram might also

represent a set of localities more or less affected by adverse ecological conditions. (In the case of marine organisms, as in this paper, these conditions will be related mainly to either latitude or depth.) The likelihood of an ecological rather than a historical interpretation can only be resolved by treating the cladograms as hypotheses of either possibility or a combination of both. They can then be compared with independently derived geological histories and with geographical patterns of ecological parameters (e.g. sea water temperatures). However, for the sake of the remainder of this discussion, we concentrate on purely historical interpretations of PAE cladograms, and defer further ecological discussion of Lundberg rooting until p. 288.

For the purposes of the palaeogeographical and tectonic aspects of historical biogeography, we are only interested in historical events that simultaneously affected large numbers of taxa within an overall biota. Although some divergences in sample locality cladograms will be based on large numbers of taxa (cf. characters in phylogenetics), this will not be so for all divergences. Corroboration of inferred events should therefore be sought in congruences amongst the cladograms of as many different sample groups as possible. Ecological factors arise again here, because there is a higher probability of congruence amongst groups which share similar broad ecological limits and similar dispersal ecology. On the other hand, in order to avoid ecological prejudgement, it is probably better to disregard ecology and to sample different groups of organisms heuristically. As in cladistic biogeography, the recognition of congruent patterns of distribution amongst different taxonomic groups is in itself very strong evidence that they have resulted from the same major historical events, like tectonics or climatic change, regardless of ecological assumptions. The possibility that the same patterns have arisen by chance becomes negligibly small as congruence increases (Nelson and Platnick 1981, p. 503).

So far, we have only considered divergence of biotas, but major historical events can also result in convergence (sometimes also called intermixing or integration of biotas). It might seem that because our method only gives a dichotomous pattern indicative of divergences, it cannot detect convergences. In fact, information about convergences is present in PAE cladograms but is 'cryptic', though Dr Peter Forey (pers. comm.) has pointed out that several PAE cladograms showing congruent polychotomies might indicate convergence. Our method nests

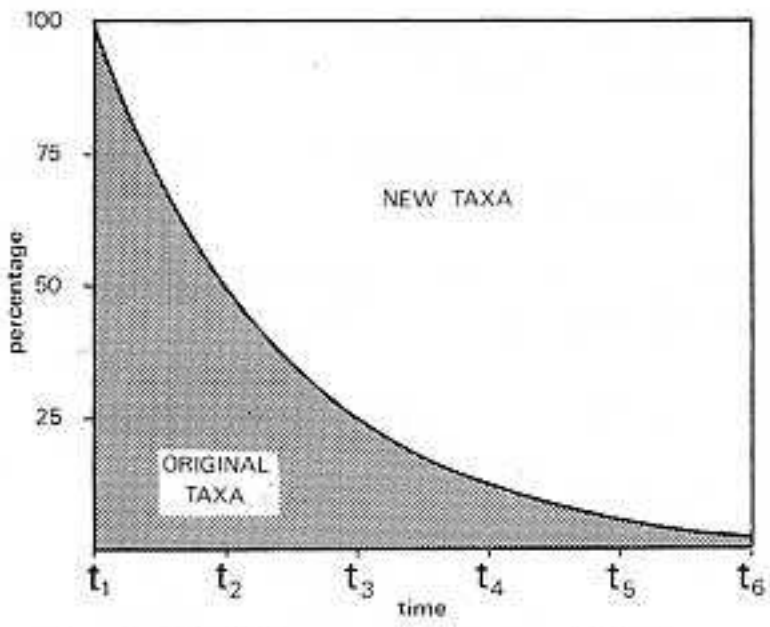

FIG. 1. Model for a constant rate of biotic turnover, shown in terms of a survivorship curve for an original assemblage of taxa (see text below).

sample localities according to how recently they have shared a common biota, irrespective of the real history of convergent and divergent events. To help understand how PAE treats a mixed history of convergences and divergences, it is best to refer to a hypothetical model of changing biotas affected by major historical events (Figs 1 and 2). Note that we are using this model, not as a representation of envisaged processes, but simply to provide a fictitious biogeographical history for demonstrating how our method would perceive it.

As with all models, some initial assumptions have to be made.

1. We have assumed that chance dispersal between areas is insignificant.

2. We have incorporated a major event which affected biotas between each time plane sampled, and have made these alternately convergent (i.e. barrier breakdown) and divergent (i.e. vicariance).

3. We have assumed a constant biotic turnover which is intended to represent the net effect of originations and extinctions of taxa, whether in response to major events, phyletic gradualism or any other factors. Our assumed turnover rate is such that half of the taxa present at one time plane have become extinct and been replaced by new taxa by the next time plane (Fig. 1). For genera of echinoids, this would mean that sampled time planes are approximately 20 to 30 million years apart.